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A Descriptive Analysis of Porcupine Scavenging in an Experimental Forensic Context

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A DESCRIPTIVE ANALYSIS OF PORCUPINE SCAVENGING IN AN EXPERIMENTAL FORENSIC CONTEXT

by

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Addressing the impact of scavengers is essential for a complete analysis of many forensic sites. Despite considerable research on canids and rodents on a broad taphonomic scale (Haglund 1992; Haglund et al. 1989; Haynes 1983), the North American porcupine (*Erethizon dorsatum*) has not been studied for its impact in forensic contexts. In order to address this research gap, I will explore the role of the porcupine in scavenging bone based on data collected during a recent experimental taphonomic study (Sorg 2013). Funded by the National Institute of Justice, this study included data from motion- and heat-sensitive cameras focused on domesticated pig (*Sus scrofa*) cadavers exposed in the western Maine woods between 2010 and 2012. Using the photographic and videographic evidence of scavenger visitations at two of these sites, I will examine the behavior of the North American porcupine each time an animal of that species visited the remains. I will compare their observed behavior to the literature regarding porcupine behavior and the behavior of other scavengers, including rodents and canids. Finally, I will compare porcupine dental morphology to the tooth-marks left on the remains to address the possibility of identifying porcupine-scavenged remains in forensic contexts.

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INTRODUCTION

Mammalian scavengers significantly impact many forensic sites in patterned ways, redistributing and modifying remains. While addressing the complexities of applying archaeology in forensic contexts, Haglund lists five "specific challenges to the death investigation" including "(1) locating the remains; (2) maximizing their recovery; (3) assessing special and temporal relationships relative to their death, burial or dispersal; (4) differentiating ante-, peri-, and post-mortem movement and modification sequences and (5) interpreting information from the scene context" (2001:28). In order to achieve these goals and generate inferences regarding the distribution of remains and estimations of time since death, a complete taphonomic analysis must include a comprehensive understanding of scavenger activity.

Although many forensic and archaeological studies have focused on the effect of rodents and canids on bone modification and redistribution, no study has emphasized the role of the North American porcupine (*Erethizon dorsatum*). Observations of the North American porcupine modifying bone are rare within an ecological context and nonexistent in forensic literature. Since behavior within taxonomic groups can vary significantly with regards to seasonality and foraging behavior, different species are likely to interact with remains in distinct ways. Thus, research on other members of the order Rodentia cannot be assumed to apply to the porcupine without further study.

During an experimental study in Maine, seven pig (*Sus scrofa*) cadavers were placed in forested areas to observe the impact of various taphonomic factors, including

scavenging activity, on the remains (Sorg 2013). Using data collected from motion- and heat-sensitive cameras at two of the pig sites, I explored the behavior of the North American porcupine (*Erethizon dorsatum*) as it visited and modified those sites. I then compared this observed behavior with anticipated behavior based on the ecological literature and previous forensic and archaeological research on Rodentia.

During the taphonomic study, the remains of a pig femur and a mandible were recovered, both with damage directly attributable to the porcupine. I examined the gnawing damage in conjunction with the literature on dentition and Rodentia bone modification to explore the possibility of identifying porcupine activity at specific forensic sites. I will also compare the porcupine's bone modification with the generalizations regarding rodents to determine if this distinction is essential or useful when encountering remains impacted by an unidentified member of the order Rodentia.

In the following sections, I will compare the literature on porcupine and Rodentia behavior to the behavior of porcupines observed during my research to address similarities and differences that may affect their impact on forensic sites. I will then explore the possibility of identifying porcupines at a site based on their gnaw marks by incorporating my measurements of incisor widths and measurements of gnaw marks on collected bone fragments. I hypothesize that scavenging by the North American porcupine differs from scavenging by other Rodentia, and distinguishing remains scavenged by porcupines in forensic contexts is possible using certain characteristics diagnostic of the North American porcupine.

LITERATURE REVIEW

Prior Forensic and Archaeological Research

Both archaeological and forensic research on bone modification has been essential in order to separate human and nonhuman agents, resulting in a wealth of detailed diagnostic information (Bonnichsen and Sorg 1989; Fisher 1995; Haglund, Reay, and Swindler 1989; Haglund 1992; Haynes 1983; Pokines 2014). Several phylogenetic groups, such as the felids, canids, and rodents, have distinct, documented patterns of gnawing damage (Fisher 1995; Kerbis Peterhans 1990; O'Connor 2000). However, little research has focused on identifying these patterns within narrower phylogenetic groups, and only recently has research turned towards more holistically addressing the predictability of scatter patterns at sites by incorporating local ecological information (Kjorlien, Beattie, and Peterson 2009; O'Brien et al. 2010; Young et al. 2014).

In North America, canids have been studied the most extensively, and wolves the most particularly, but most of the research has been done by Haynes (1982; 1983) and Haglund, Reay and Swindler (1989). Haynes (1982) focused specifically on the wolf *(C. lupus)*, placing its feeding behavior in a year-round context of mating and denning. He distinguished between the utilization of scavenged carcasses separately from freshly-killed prey carcasses, describes five elemental groupings scavenged on "as units" (269), and examines the gnawing damage done to most major bones in the context of a "winter feeding sequence" (271). His analyses focused on large herbivore carcasses with minimal human involvement. Haynes (1983) compared the gnawing damage of the wolf

with several species of Ursidae, Felidae, and the Spotted Hyena (*Crocuta crocuta*), supporting a felid-canid distinction, distinguished largely by minimal puncture marks by felid incisors and heavy gnawing by canid molars. These patterns correspond with the foraging habits and dental morphology of each taxonomic group.

Of the Rodentia, Old World porcupines (Hystricidae) and small rodents have been studied copiously, while the New World (Erethizontidae) North American porcupine (*Erethizon dorsatum*) has been almost entirely overlooked in skeletal contexts. Since Old World porcupines have long been of great interest archaeologically, their bone modification and collecting habits have been well documented (Alexander 1956; Dart 1958; Kerbis Peterhans 1990; Kerbis Peterhans and Singer 2006; Pokines 2014). By contrast, although North American porcupine has occasionally been observed gnawing on bone (Curtis and Kozicky 1944; Roze 2012), its impact on forensic and archaeological sites is never discussed.

Pokines (2014) compared bone modification from large and small rodents, but did not distinguish between Old World porcupines (Hystricidae) and the North American porcupine (Erethizontidae). Yet, these porcupines are taxonomically distinct, occupying different branches of the Rodentia order, and differences in their habitat, behavior, and morphology (Roze 2012) indicate that inferences about one family cannot be reliably drawn from the other. Members of each family occupy distinct ecological niches. For example, the New World porcupines are arboreal while the Old World porcupines are not, despite both inhabiting a similar range of habitats from a wide range of forests to open countryside. This appears to significantly alter their behavior regarding the collection of bone, and there appears to be no evidence of the collection of bone by New

World porcupines, while extensive research has identified bone collecting behavior in Old World porcupines. I believe this distinction sufficiently eliminates the possibility of directly applying any research into Old World porcupines to studies of New World porcupines.

Since bone modification of small rodents in forensic contexts has been definitively observed in North American contexts (Haglund 1989, 1992; Klippel and Synstelien 2007), this could indicate that the rarity of bone gnawing by larger rodents is more a result of research biases, and the relative population density of each species, than the improbability of the behavior itself.

Previous research demonstrates that animals affect remains in patterned ways. Classifying scavengers by genus or family provides insight into their impact on remains, but variations in behavior are necessarily broad generalizations. Haglund et al. (1989) stated that most elements scattered by canids will be found close to the origin of the site and along animal trails, but Haynes (1982) described wolves transporting bone to secondary locations called "rendezvous sites" (267) or back to their den for pups. Although in this instance Haynes described hunted carcasses not scavenged carcasses, knowledge of such behavior and the association of wolves specifically scavenging remains could lead a forensic team to search for such a wolf den or rendezvous point in order to recover more elements. Similarly, identifying particular patterns of other scavengers may allow for more specific inferences when analyzing forensic sites.

In an article on postmortem rodent activity, Haglund (1992) stated that species-level identifications of rodents at forensic sites, in conjunction with information regarding

their seasonal behavior, may aid forensic investigations by determining when the damage occurred, which could improve estimations of the postmortem interval.

Bone Modification by Rodents

Rodents gnaw on bone both for nutritional intake and to sharpen their incisors, though the motivation may vary depending on whether the bone is fresh or dry (Pokines 2014). Rodent modification is often easily identifiable as "paired, broad, shallow, flat-bottomed grooves on the densest parts of a skeleton" (Klippel and Synstelien 2007, 765). Usually, these gnaw marks are reflected as "long, relatively regular rows," but they may also "occur as a set of irregularly oriented grooves" (Fisher 1995, 40) with "disorganized striae overlying each other" (Haglund 1992, 1460). Individual tooth marks are directly attributable to their distinct "chisel-like incisors," and are "shallow and small" (Fisher 1995, 40). Concentrated gnawing damage "can eliminate bony crests, ridges, and protrusions or create sizable troughs or cavities" (40). Haglund (1992) noted that identification of rodent species based on gnaw marks is "unreliable," but species-level identification may be possible by using scat or hair left at the site.

Whether rodents prefer weathered bone free from soft tissue or fresh spongy bone is uncertain, but both have been observed in literature (Haglund 1992; Klippel and Synstelien 2007; Young et al. 2014). In the Midwest, Nawrocki (2009) claimed that rodent gnawing is rare in the first year postmortem because the bone is not dry enough, which may be typical of the array of rodent scavengers found in the midwestern United States rather than indicative of a taxonomic pattern, since Haglund observed activity very soon after death in Washington state (1992).

There is also little consensus regarding which elements rodents favor (Klippel and Synstelien 2007). In several forensic case studies, Haglund (1992) observed small rodent damage to the supraorbital margins and nasal apertures of the crania. However, for smaller rodents, Pokines (2014) noted that gnawing on fresh bone is more likely to occur for nutritional purposes, while gnawing on dry bone may occur primarily to sharpen incisors. On dry bone, this may result in gnawing concentrated on "thinner, already exposed margins" (238) or "sharp margins of dense bone" (236), while gnawing on fresh bone is more likely to result in exposed sections of cancellous bone near the epiphyses.

Rodent behavior is noticeably different across species. Klippel and Synstelien (2007) observed that brown rats favored fatty cancellous bone and "[their] modifications…bear only slight resemblance to typically reported rodent damage," while eastern gray squirrels gnawed on "thicker bone cortices only after fats had leached away" and more closely resembled typical rodent damage (765). Young et al. (2014) also observed similarly differential activity between wood mice and squirrels.

In general, Pokines (2014) claimed that porcupines, including Old World species, and other large rodents "leave broader, flatter (and deeper) gnaw marks…concentrated on the margins of elements…often [obliterating] distinct furrows, leaving a more even margin" (234-35). He claimed that larger rodents prefer drier bone and will not consume soft tissue, and some species will sometimes transport larger elements to dens. Large rodents do not discriminate based on the taxonomic source of the bone, and will cause heavier damage to bone. In addition, Pokines stated that the goal is both nutritional intake and incisor sharpening, and he asserted that porcupines will avoid human contact, thus limiting their role in forensic contexts. However, Roze (2009) claimed that New

World porcupines possess more "boldness and self-confidence" (201) around humans than Old World porcupines, which may invalidate Pokines's assumption for North American porcupines and increase the likelihood of porcupine-scavenged human remains.

Local bone displacement by rodents is common, but distant scatter is only likely to occur with specific species, in particular packrats (*Neotoma* sp.) and Old World porcupines (Pokines 2014).

Dentition

Rodents have "four very large, sharp incisors" that "slice and chisel both green and woody vegetation or gnaw at wood, bones, or anything short of metal" (Elbroch 2006, 43). These open-rooted teeth continuously grow in height to retain a sharp surface and must be worn to "maintain a functional height" (Reitz and Wing 1999, 48). Rodents lack canines (Elbroch 2006, 47), and possess "molariform" teeth, rather than distinct premolars and molars, for "crushing and grinding…tough plant and mast fibers" (48). Rodents leave particularly distinct patterns, working "along the edges of a bone in a very systematic manner, leaving rows of tooth-marks which, on close examination, clearly reflect the paired chisel-like front teeth typical of a rodent" (O'Connor 2000, 38).

One consideration for differentiating within a genus is the relative size of each species. When assessing bite marks, this can be an obvious tool for separating porcupine from mice, and coyote from foxes. O'Connor (2000) cited an example where the size of the measurements indicates that the teeth are "consistent with the black rat *Rattus rattus*" (38), though smaller rodents pose significant challenges to identification in this manner

due to the wide range of species with overlapping incisor widths. Osburn and Cramer (2013) used incisor width to distinguish porcupines from beavers in their study, based on Elbroch's data (2006). However, Osburn and Cramer used measurements on salt-infused wood, not bone, which may influence the clarity of the markings, and they used this data primarily to exclude beaver activity at these sites.

Comparing the range of incisor and intercanine widths (Elbroch 2006) demonstrates that the differences between porcupine and beaver are likely substantial enough to distinguish them from each other when measuring the incisors themselves. However, a recent Massachusetts study by Pokines at al. (2017) suggested that, at least among rodents, there may be enough overlap between porcupine and other larger rodents (particularly the groundhog, *Marmota monax*, and the muskrat, *Ondatra zibethicus*) to prevent a direct and an immediate identification based on incisor width alone.

North American Porcupine (*Erethizon dorsatum*) Behavior

Porcupines rely heavily on their well-developed olfactory and auditory senses (Curtis and Kozicky 1944), though their vision is poor (Woods 1973). Porcupines are spread across a wide variety of habitats in Canada and the United States, though they are restricted to high-vegetation areas for foraging (Roze 2012; Woods 1973). Their diet of fresh tree leaves supplies sufficient amounts of water, so the porcupine does not require access to a water source (Roze 2012). The porcupine chooses its home range based on the selection of trees and shows a significant preference for some varieties over others (Coltrane and Sinnott 2013).

They are generally nocturnal, though Roze (2012) noted that the North American porcupine is "less photophobic" than its counterparts, and it will spend time in early spring foraging in "bright daylight" (29), though it returns to nocturnality in late spring and summer. Griesemer (1998) estimated the porcupines spent less than 13% of their time on the ground, though Roze (2009) noted that ''ground-feeding' behavior varies widely by geographical region.

Gabrielson (1928) also noted that porcupines in Oregon quickly return to shelter "at the first wet weather" (38), and Roze (2009) observed a similar aversion to rain. Woods (1973) claimed that they do not defend territory, although they "urinate in paths, near dens, and at the base of trees," and they will defend their "feeding trees" (3). Porcupine are often solitary, but have been found in pairs (Woods 1973), often but not always of the opposite sex (Curtis and Kozicky 1940, Roze 2009), typically in winter months when they may share a den (Woods 973). However, Roze (2009) noted that this happens infrequently and does not last longer than a week, with "clear indications that the experience is unsettling to both animals" (116), marked by heavier territorial scent marking, increased 'squawking' noises, and in many cases abandonment of the den by both animals following the den sharing period. Den sharing is likely more common in areas with lower concentrations of dens (Roze 2009, 117).

Dens may be reused each year, especially when in rock formations, but in Maine, dens often take the form of "a hollow log, a windfall, or an upturned or loosened tree root system" (Curtis and Kozicky 1944, 139). Alternatively, they may occupy 'station trees' in winter, which are used on occasion when no den is available (Curtis and Kozicky

1944; Woods 1973). In Maine, 'station trees' are predominantly hemlock and white spruce (Curtis and Kozicky 1944).

Although they do not hibernate, they are less active in colder weather (Woods 1973). In central Massachusetts, Griesemer et al. (1998) reported that during the day, porcupines were found in dens during colder months (November to April), and in trees from May to October. In the Catskills, Roze (2009) noted that porcupines predominantly occupy dens beginning in late October or early November, after temperatures have fallen below freezing for between 3 to 9 days. Porcupines emerge from their dens in late winter or early spring when temperatures are above freezing and snow cover is gone.

Mobility and Home Range

Coltrane and Sinnott (2013) stated that "porcupines tend to use specific core areas and dens within their home range and have relatively small daily movements" (511). Travel tends to occur "underneath windfalls, dense cover, and leaning trees rather than over them" (Curtis and Kozicky 1944, 139), and they may travel up to 330 feet between their den and food, using the same trail other animals have left. Porcupines do not prefer water, but will swim across smaller bodies (Woods 1973). It is not uncommon for them to tunnel through the snow in winter (Curtis and Kozicky 1944), though they do not otherwise burrow into the ground (Roze 2012).

In winter, they stay closer to their dens, particularly in very cold weather and with much snowfall (Curtis and Kozicky 1944; Roze 2012; Sweitzer 1996; Woods 1973), with 59% of feeding in Maine occurring within 200 feet (61 m) of their den (Curtis and Kozicky 1944). Roze (2009) noted the winter home range averaged 7.4 ha (18.3 acres)

compared to the summer range of 64.9 ha (160.4 acres), and snowfall presents a major obstacle for travel in winter. Griesemer et al. (1944) observed the average winter distance to be 33.5 m in central Massachusetts, though this increased to 58 m when the porcupine sought new feeding trees. Tenneson and Oring (1985) found that porcupines expanded their home ranges in mid-February, possibly to expand their range of resources during the scarce season.

In Alaska, Coltrane and Sinnott (2013) determined a porcupine could travel 2.5 km in 24 hours, and a Minnesota study found that males moved an average of 21 meters per day, while females moved 11.6 meters per day, though movement was strongly correlated with wind speeds (Tenneson and Oring 1985).

The adult male's home range can significantly expand during mating season, as when one porcupine in Roze's (2009) study expanded its summer home range of 19.9 ha (49 acres) to 100 ha (247 acres). Adult male ranges will overlap with several females' ranges, and may overlap with other males, and their ranges may vary significantly in size depending on maturity and dominance. By contrast, females will "exclude other females from their territories," their territories are approximately equal in size, and they demonstrate "strong site fidelity" to their home range (160-2).

Several researchers have studied the home range of the North American porcupine, with significant regional and seasonal variability. In Sweitzer's (2003) study on breeding movement of porcupines in the Great Basin, he also found that dominant male porcupines roam over larger expanses during the breeding period, and their home range typically overlaps that of multiple females and other males (2003, 2). Dominant males ranged over an average of 20.7 hectares (0.207 km^2), while subordinate males

ranged over 2.9 ha (0.029 km^2), and adult females ranged over 8.2 ha (0.082km^2) on average. Coltrane and Sinnott's (2013) study in Alaska hypothesized that home ranges would be larger than those in temperate regions due to "decreased diet quality and increased average body size" (506). The average home range size for male porcupines was 2.77+/-2.75 km² and for females was 0.94+/-1.64 km² (508). Roze's (2009) study of home range is more likely to reflect that of porcupines in Maine, though Alaskan porcupines most likely experience the largest range.

Foraging Habits and Salt Drive

Coltrane (2012) defined the North American porcupine (*Erethizon dorsatum*) as a facultative specialist herbivore. Its diet is composed primarily of "buds, foliage and mast," and only some bark (Griesemer, Fuller and Degraaf 1998, 275), although this varies seasonally and regionally (Roze 2012). In winter, their diet includes less protein and more fiber, which consistently leads to significant weight loss (Coltrane et al. 2011; Roze 2012). Winter foraging is more opportunistic than in summer, though still largely selective (Roze 2009). Roze (2009) noted that juvenile porcupine scrape marks differ from adults in neatness and consistency, and classifies them as "messy eaters" (125).

Increased nutritional needs are likely to drive porcupines to more dangerous foraging patterns. In a Nevada study, Sweitzer (1996) cited nitrogen and protein deficiencies in winter leading to riskier food collection strategies. He also noted that smaller porcupines "avoided foraging in high-risk, open areas that were regularly used by large porcupines" (1069). Predation was highest in late winter, when porcupines were "nutritionally stressed" (1074) and more likely to forage in open areas.

Roze (2009) studied the porcupine's salt drive and noticed that the porcupines "[treated] the salthouse as a sodium buffet, moving at regular intervals to sample new sticks for shorter or longer periods" (71). When two porcupines were in the area together they "maintained a wide spacing between themselves" (70). Additionally, Roze noted that they licked the salt sticks as they chewed, "monitoring sodium levels continually with their tongues," and they did not visit during rainy nights, likely because the rain "leached out surface ions and made all natural salt sources unattractive" (71). Seasonally, Roze noticed that visits to the salthouse ceased "almost entirely between November and March, only to resume with explosive force in April and May…then [declined] through midsummer," with a "secondary peak" between August and September (71). The sex ratio skewed significantly towards females with offspring that year, who made several repeat trips over sometimes challenging terrain, up to 1 km, likely due to an increased need while nursing. Males visited on the same seasonal schedule, though with considerably less frequency.

Roze (2009) postulated that the April-May surge may be a result of the porcupine abandoning its winter den and a lack of access to sodium in winter rather than a reduced sodium drive in winter, which may leave the possibility of winter sodium-seeking open within a reduced radius. Also, Roze correlated the secondary August surge with a "period of apple-feeding" (75) in the Catskills, resulting in a greater need for sodium, which would likely not occur in areas where the porcupine does not feed predominantly on apples during this period.

Porcupines will also seek salt by swimming to aquatic vegetation, such as water lilies. Roze (2009) once observed that the long bones of a recently killed deer had been

scraped by a porcupine, though this has only rarely been noted in the literature related to the North American porcupine. Porcupines also frequently seek salt from man-made sources.

There is some evidence that porcupines will carry plant material to a separate den-like location. A study of porcupines in Oregon suggested that females bring tree limbs back to their den, most likely to feed young based on the smaller teeth marks found on the limbs (Gabrielson 1928), and a study comparing *Neotoma* middens with porcupine middens in the western United States suggested "some limited caching occurs in winter" (Betancourt, Van Devender and Rose 1986, 271). Also, an Alaskan archaeological study noted that charred wood had been transported into a cave by porcupines (Dixon 1984).

Reproduction

Mating occurs from October to November, with male porcupines spending several days in the company of a female before mating, then re-dispersing (Roze 2009). The female is only in estrus once a year for 8 to 12 hours, and the gestation period is approximately 16 weeks or 210 days. One pup is born between May and June, and they can consume vegetation within two weeks of birth (Woods 1973; Roze 2009), though nursing continues nightly for four months, which imposes a "significant metabolic cost" (Roze 2009; 2012). Porcupine pups tend to gain weight rapidly in order to prepare for winter (Roze 2009).

Young porcupines progressively gain independence beginning around 3 months old (around August-early September), spending some nights a short distance apart from their mother (Roze 2009). Although they remain fairly close to each other, the number of

nights spent together progressively decreases through the end of October, when "long-distance separation occur[s]" (Roze 2009, 156). In the fall, juvenile females tend to disperse while males remain (Roze 2012).

Response to predators

Osburn and Cramer (2013) tested the porcupine's response to the scent of generalist and specialist predators at sites of salt-infused wooden stakes. While porcupines demonstrated a strong avoidance of fishers, which "possess a unique hunting and killing technique to prey upon porcupines" (67), their aversion to coyotes was significantly lower, suggesting that they did not consider coyotes as strong of a threat. However, the control sites without any scent were visited more frequently than those with any scent of predators, indicating that porcupines may still attempt to avoid coyotes when foraging.

Purpose of Bone Gnawing: Salt Drive vs. Incisor Attrition

New World porcupines consume "tree leaves, fruit, and tree bark" (Roze 2012, 20). The typical diet of the North American porcupine is so rich in calcium that it "must be excreted in the urine" (118), but it significantly lacks sodium. Additionally, as with many herbivores, the porcupine's potassium intake is high (Roze 2009). As in any animal, when the ratio of potassium to sodium climbs too high, a porcupine will begin to display "apathy and lassitude as nerve and muscle functions decline, followed by weight loss" (67) ultimately leading to death. Thus, the porcupine has a strong drive to seek sodium.

Bone from a freshly killed deer contains roughly a quarter of the sodium content of the carcass, and porcupine have been observed feeding on the leg bones of a "recent deer kill" (Roze 2012, 118). Roze added that porcupines may feed on other parts of the carcass, but "bones are usually all that is left after other scavengers finish with a carcass" (118). He also noted that bone chewing occurs more frequently in phosphate-depleted regions, and that the drive for sodium varies depending on sex and season.

While dental attrition is also necessary due to the porcupine's open-rooted incisors, the tree bark in its diet may fulfill that need sufficiently. Woods (1973) calculated porcupine incisor growth at about 1.5mm per week, with 315 mm 'worn away' each year. Lower incisors grow more rapidly, and incisor growth in males occurs more quickly, possibly due to the "habit of chattering [their] teeth when disturbed" (Woods 1973, 2). Roze stated that "Although each incisor loses 100% of its length to wear in a year's chewing, its length always remains the same" (2009:48), and no instances of malocclusion have been noted (Elbroch 2006). Additionally, Capello classified porcupines as Hystricomorph rodents, similar to the guinea pig and chinchilla, which have low rates of malocclusion (2006).

Thus, the most likely explanation for bone gnawing is a nutritional need for sodium, which also drives porcupines to destroy man-made objects, such as rubber tires, and venture closer to roads which have been salted, possibly leading to increased casualties. This suggests that any additional need for incisor attrition is minimal and would not be a primary drive for bone chewing.

METHODOLOGY

The North American porcupine (*Erethizon dorsatum*) featured prominently at two sites in Sorg's (2013) taphonomic study. At both sites, cadavers of domesticated pig (*Sus scrofa*) were placed in forested areas one mile apart in western Maine on October 20, 2010. The cadavers were clothed in pants and a shirt to convey some human scent. Motion- and heat-sensitive cameras were focused on each cadaver in order to capture any movement by scavengers in the form of photographs and corresponding 10-second videos. Data loggers were also placed at each site to capture information on humidity and temperature.

At Site M, heat and motion-sensitive camera data were collected until May 21, 2012, while at Site N data were only collected until November 21, 2011. (After November 21, 2011, photographs at Site N were taken at hourly intervals instead of capturing activity based on motion-sensitivity. These data did not allow me to track porcupine activity at this site and were excluded from my research.) Approximately 200 videos and photographs out of 2,400 collected at Site M featured porcupine activity. At Site N, over 50 out of almost 6,000 videos and photographs demonstrated porcupine activity.

Using these data, I tracked behavioral and environmental variables associated with each porcupine visitation. Environmental factors included temperature, precipitation, snow cover, and light. Behavioral factors included the behavioral event, the number of animals, and when possible, the type of bone element affected.

Since the motion-sensitive cameras offered limited insight into the state of the remains at the site during the periods of porcupine activity, describing the state of the

remains during each porcupine behavioral event was impractical. However, I used the photographs that other researchers and I took during sporadic visits to the site to provide a descriptive context for the porcupine activity. At both sites, this included one visit prior to any porcupine activity and two to three visits during and after. Using these photographs, I described the state of the remains, including overall decomposition, skeletonization, and scatter. I incorporated this information into my analyses, essentially discussing porcupine modifications of bone elements in blocks of time.

I then connected literature on behavioral patterns, including seasonality, salt drive, and mobility, to the observed behavior at each site. With this information, I assessed whether associations can be reliably drawn between their generalized behavior in research and their observed behavior.

Finally, I considered the dentition of the porcupine and compared it to the markings on a femur and a mandible gnawed on at Site N and collected. I compared measurements of these markings and measurements of porcupine and beaver teeth from the University of Maine Zooarchaeology Laboratory to measurements and studies in literature to address the possibility of distinguishing porcupine from other scavengers at forensic sites based solely on gnawing damage on bone.

The number of photographs and videos featuring porcupine activity was relatively small compared to the overall number of scavenging photographs, and only two bone elements demonstrating porcupine modifications were collected. However, the dataset allowed for numerous behavioral and environmental variables to be examined. In order to comprehensively address the impact of these variables on observed porcupine activity,

I approached my analyses descriptively rather than statistically. This allowed me to explore a wider variety of variables in more depth than a statistical approach would offer.

Porcupine Visitation Variables

Quantitative Variables

For each porcupine visitation, I noted the date, time, and temperature in degrees Fahrenheit. Additionally, the number of porcupines in the photograph could be easily observed, though individual porcupines could not be identified.

Behavioral Events

The behavioral event, or the type of activity the animal engaged in, was separated into three hierarchical levels: passing by, sniffing/exploring, and gnawing. Additionally, on two occasions, the porcupines interacted with each other and on one occasion, the porcupine was at the site at the same instance as a coyote, resulting in a fourth miscellaneous behavioral category. Although the visiting animal may have been engaged in a higher level of activity during many visits, I minimized speculation and maximized consistency by categorizing each event only at the highest level of activity that I could definitively observe.

"Passing by" was identified by the animal's presence in a single photograph within a sixty minute window, with no video or photographs indicating that they were interested in the remains at the site. Thus, I classified this behavior as the animal traveling past the site rather than stopping at the site. "Sniffing/exploring" was

characterized, minimally, by a photograph with the animal postured in a manner indicating their attention was on the remains at the site. Alternatively, I also classified their behavior as sniffing/exploring when several photos or a video indicated that the animal lingered in the area more than 2 minutes. "Gnawing" behavior was indicated by the animal making direct contact with a particular element identifiable as bone. Initially, an additional category was created for moving bone, but the porcupine was not observed walking away with any bone, though it did pick up bone to gnaw.

Affected Bone Elements

In some instances, I was able to observe a porcupine in contact with a particular type of bone, such as a mandible, a rib, or a pelvis. However, in most other instances, the identification was highly subjective. Since the pig cadaver was a juvenile, many bones remained unfused, increasing the challenge of identifying specific elements. In multiple cases, I was able to identify a bone as a "long bone shaft," rather than as a femur or humerus. When the bone was too small to identify, I labeled it as a "small bone." When I could not observe which bone the porcupine interacted with, I labeled it "unknown." This last category primarily arose when I observed the porcupine gnawing on an element that was too close to the ground to determine its shape, or when it was obscured by other elements.

Other Environmental Variables

Precipitation was identified by its presence or absence. In videos during other scavenger visits, rain was visible. However, in no instances did the porcupine visit while rain or snow fell.

Snow cover was classified as present or absent, then described by depth. Since there was no objective way to determine snow depth, I estimated it by sight and classified it as minimal (0-1 inch), light (1-3 inches) and heavy (over 3 inches).

Daytime or nighttime was also loosely categorized as such. Generally, I determined this based on whether or not the photograph was in color, or in black and white, indicating the camera had switched into a nighttime mode.

Faunal Lab Measurements

Using samples from several species in the University of Maine Zooarchaeology Laboratory and Elbroch's (2006) research on animal skull morphology, I compiled data on incisor width for the North American porcupine and the two animals with the closest incisor widths: the American beaver (*Castor canadensis*), and the woodchuck (*Marmota manox*). Elbroch's measurements were taken "parallel to the occlusal surface," which I used as a guideline for my own measurements. First, I used dental calipers to measure the greatest width along the mid-shaft of the incisor, on the exposed region just anterior to where the alveolar margin would be. Noticing varying wear patterns on the tips of the incisors, I then measured as close as reasonably possible to the occlusal surface, and parallel to it.

I collected data from five porcupine, one woodchuck, and two beaver. All samples appeared to be from adult specimens. I measured one complete set of incisors from a woodchuck and beaver, and one additional pair of upper incisors and one lower incisor from two separate beaver specimens. One complete incisor set, upper and lower, was measured for the porcupine, but most incisors were in pairs. Altogether, I measured three pairs of upper incisors, two pairs of lower incisors, and two individual lower incisors, from five different porcupines.

Porcupine Modification Measurements

Fragments of the mandible and the femur from Site N were collected in late October 2011. A porcupine was seen gnawing on each element, and no other rodents were found at the site, so the patterns of gnaw marks on the bone are indisputably porcupine. The gnaw marks also clearly resemble rodent bone modification, with well-defined, parallel striations. Based on this, I examined each bone fragment and took measurements in several areas with more distinct grooves in order to assess the possibility of deducing porcupine gnawing based on the width of the tooth marks. Measurements were taken with dental calipers between the peaks of the ridges.

RESULTS

Site M

This pig was placed on October 20, 2010. Temperatures after that ranged in from about 26°F to 49°F until the first snow fell on November 1st. Minimal decomposition and no insect or scavenging activity were apparent until April 2011, and by May 17, 2011, the remains were mostly skeletonized with some articulation. Almost complete skeletonization and disarticulation had occurred by June 28, 2011. The area was forested, with canopy cover estimated at 78% on October 20, 2010, and at 62% on June 1, 2011. Local foliage consisted primarily of oak, striped maple, red maple, sugar maple, and bracken fern, as well as some small fir, striped maple, gray birch, and white pine. In June 2011, the bracken fern was knee to waist high.

Scavenging (by animals other than porcupine) did not begin until April 26, 2011, although a bobcat passed by the site in winter. Turkey vultures (*Cathartes aura)* frequented the site for most of May; this species was the primary scavenger. Rabbits *(Lepus americanus)* sporadically visited the site and on one occasion a raccoon *(Procyon lotor)* visited. These visitations occurred prior to any porcupine activity.

The last site visit by researchers prior to any direct porcupine interaction with the bones occurred on June 28, 2011. While this site had little leaf litter, several ferns obstructed the view of some of the smallest elements, but most elements were easily visible. The shirt and pants were puddled approximately where the torso and pelvis once were, with multiple ribs and some vertebrae. The shirt, ribs, and multiple vertebrae were located over a puddle of dissolved soft tissue, the densest part of the decomposition

island, with clumps of hair still visible. By June 28th, a fuzzy gray substance reminiscent of mold covered most of the shirt and the region immediately around it, including the margins of bone closest to the ground and in contact with the shirt. The bones clustered within this area were slower to dry on the surfaces in contact with the decomposition island and hidden under the shirt, while most of the other elements were beginning to dry and weather at this point. Several beetle larvae and flies were visible around the decomposition island.

The cranium and mandible were located within several feet of the origin, but many other elements were dispersed or missing. Vertebrae and long bones were scattered and rarely found in clusters. One half of the pelvis was no more than two feet away from its origin, but the other was an additional one to two feet beyond that, with a femur. Missing elements included the sacrum, a femur, the anterior limbs, and the scapulae. No damage attributable to mammalian scavenging was apparent on the remaining bone elements.

Summary of Porcupine Activity

A porcupine passed through three times in October and November of 2010, and a porcupine was seen visiting once on May 1, 2011. The next visit occurred on May 31, 2011, when a porcupine demonstrated an interest in the site by sniffing within two to three feet of the center of the remains. A porcupine was seen visiting the location once the next day, then no visits occurred until July. Between July 5 and August 24, 2011, porcupine visits to the site occurred on 26 days. However, the only observable direct contact with bone during this time occurred on July 27, August 9, and August 24.

Similar to the first year pattern, no porcupine visits occurred between November 13, 2011 and March 26, 2012, although the remains were skeletonized, weathered, and scattered at this point.

In 2012, two visits occurred in late March, nine in April, and four in early May (**Figure 1**). In none of these instances was any direct contact observed, though in several the porcupine appeared to be gnawing on local vegetation. During one instance on April 19th, two porcupines were observed sniffing around the area, one significantly smaller than the other, suggesting the pairing was a mother and her baby.

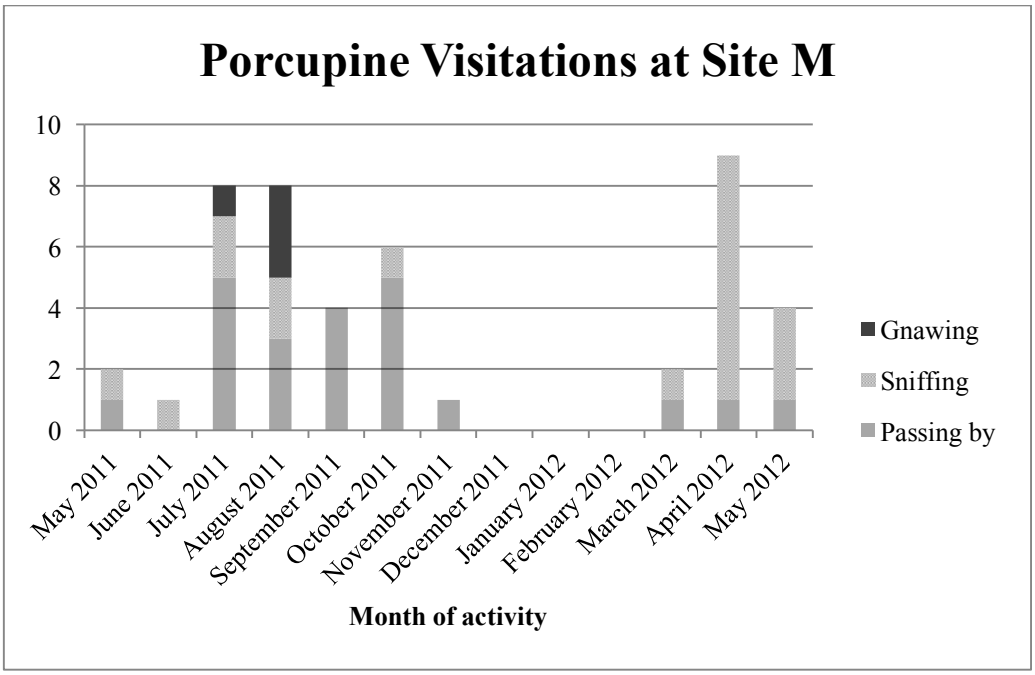

Figure 1. Number and type of behavioral events between May 2011 and May 2012 for porcupines at Site M.

All but two porcupine visits occurred at night. The first occurred on July 27, 2011 at 7:37 PM, during which the porcupine was very actively gnawing on a mandible. Since sunset on July 27th was at 8:10 PM, and light is visibly low in the video footage,

this could easily be classified as twilight. The second occurred on May 4, 2012, but the animal was only captured in one photograph, indicating it was only passing by the site.

No visits occurred while rain was apparent. Only two visits occurred while there was any snow on the ground, one on October 30th, 2011, and one on March 30, 2012, where the porcupine was obviously sniffing around and appeared in two images seven minutes apart. In neither instance did the snow cover appear more than roughly three inches deep. Any bone remaining on screen at the time was buried under several inches of snow, and the porcupine did not interact with it. The visit on October 30th occurred after the first snowfall of the season. The visit on March 30th is the second visit in 2012, after a visit on March 26, at which point the previous snow cover had completely melted.

Other Scavenger Activity

Coyotes *(Canis latrans)* visited on nine separate days between August 23, 2011 and January 22, 2012. The first contact with bone occurred on the second visit, September 9, 2011. During each visit except the first, and on January 12, 2012, a coyote interacted directly with the bone, frequently relocating ribs and small to medium elements. On October 30, 2011, a coyote nuzzled through a couple inches of snow to move a rib and then the mandible totally off screen. On January 12, 2012, the remains were covered in several inches of snow, and the visiting coyote did not attempt to interact with the bones. However, when a coyote returned on January 22, it spent several minutes actively digging in the snow to get to the bone. During these visits, coyotes did not display any behavior obviously indicating they were specifically interested in the porcupines who visited the site, until one encounter on April 24, 2012.

Other scavengers visited the site between the porcupine visitations in 2011, but they did not obviously interact with the remains. Visits included a bear (*Ursus americanus*) on June 15 and August 10, 2011, a turkey vulture on July 15, 2011, and rabbits on several occasions.

Sequence of Bone Modification

On June 28, 2011, during a site visit by researchers, no bones had been visibly modified by any porcupines, and no bone contact had been observed on camera.

The next collection of photographs from a researcher site visit on August 19, 2011 provided some indication that porcupines had gnawed on the bone. Videographic evidence indicated that a porcupine had briefly gnawed on the mandible on July 27th, and two porcupines had gnawed briefly on it on August 9th. Photographs of the mandible taken during the site visit **(Figure 2)** showed some light gnawing along the margin of the gonial angle and inferior to the mandibular condyle. Additionally, the right horizontal ramus, on the lateral surface, just inferior to the molars, appeared to be peeling. Some adipocere is seen on the inferior edge of the horizontal ramus, but the mandible is otherwise skeletonized. Other elements may have been affected, but were not photographed during this researcher site visit.

Figure 2. Mandible at Site M on August 19, 2011 after modification by porcupines.

After August 19th, a coyote visited numerous days and moved bones around. However, though a porcupine passed through multiple times, only one more instance of direct contact with bone was observed, and the bone was unidentifiable. Photographs of site visits on April 19, 2012, and May 24, 2012 indicated that slight porcupine gnawing may have occurred on a rib and a scapula, with extensive gnawing on one long bone. However, these photographs were insufficient to conclusively attribute these marks to rodents, rather than weathering or activity by other scavengers

Site N

These remains were also placed on October 20, 2010. Temperatures ranged from 19 to 49°F before snow was first visible on November 26, 2010. No insect or scavenging

activity was apparent, and minimal decomposition took place before the scavenging activity began in February. The remains were mostly skeletonized with some articulation by May 4, 2011, with full skeletonization and disarticulation occurring by June 28, 2011. Like Site M, this location was forested, with canopy cover estimated at around 94% in October 2010. Canopy cover on June 1, 2011 was estimated at 89%, with less than 1 cm of ground litter. Local foliage primarily consisted of fir, sugar maples, white ash and hop hornbeam.

Scavenging first occurred on February 17, 2011 by raccoons. The raccoons gathered in groups of four to six and dug tunnels in the snow to access the remains. Although their heavy scavenging presence ended around April 15, 2011, raccoons did continue to visit the site. Rabbits also visited the site occasionally before and after the appearance of the raccoons. Other scavengers include raven (*Corvus corax*), skunk (*Mephitis mephitis*), and turkey vulture. The bones at this site were heavily scattered by raccoon activity in winter, prior to the first visits by the coyotes and porcupines, with several bones missing. By the first porcupine activity on May 25, 2011, raccoon activity had ceased for several weeks.

The last researcher site visit prior to any observed porcupine contact with the bone occurred on June 28th. During this site visit, much of the pelvic girdle and lower spinal column was still approximately anatomically arranged, though this bone cluster had been pulled several feet from its original site by a turkey vulture, an event which was captured on video. Additionally, this cluster of bone was fresher than most other elements, which had been exposed longer and begun to dry and weather. Some light leaf cover obstructed view of some smallest elements, but most elements were very exposed.

The shirt and pants were puddled approximately where the torso and pelvis once were. Several bone elements were missing, including the cranium and a humerus. Significant localized scatter had occurred, with several clusters of bone. The last known location of the cranium was over 16 ft (5 m) from its original anatomical position. There was no evidence of canid or rodent scavenging on the remaining bone on June 28th, based on the absence of gnaw marks.

Because of the raccoon and vulture scatter at this site, we began to use orange flags to mark the location of bone on April 25, 2011, and added additional flags on May 4th. On May 24, 2011, the day before the first porcupine visit, we replaced the flags with nails, which were visibly less obtrusive. Between April 25th and May 24th, the presence of these flags may have deterred some scavengers, such as the porcupine, from appearing at the site. While multiple visits by a raccoon occurred between April 25th and May 4th, only two rabbit and three raccoon visitations occurred between May 4th and May 24th.

Summary of Porcupine Activity

The first visitation by a porcupine occurred on May 25, 2011, when it spent several minutes exploring the site **(Figure 3)**. Although my data only extended to November 21, 2011, the last recorded visit occurred on October 29, 2011. The second visit and first direct interaction with the remains occurred on July 3, 2011, and the last interaction occurred on August 8, 2011. Between these dates, a porcupine interacted with the bone on six separate days, though most activity was concentrated on the morning of August 4 between 12:50 and 1:28 AM.

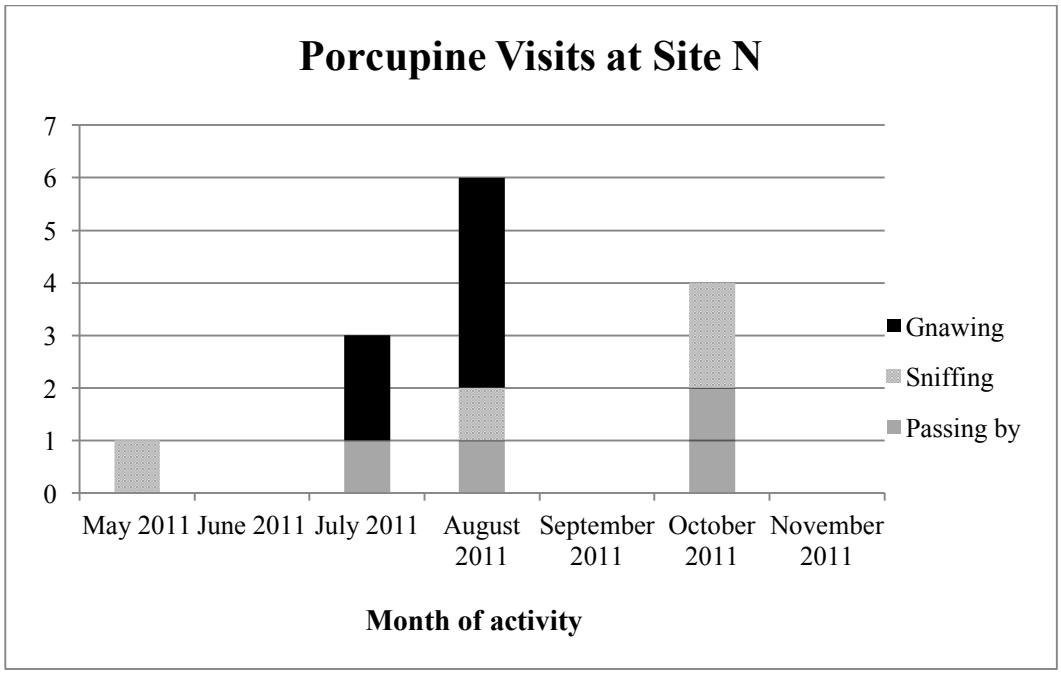

Figure 3. Number and type of behavioral events between May 2011 and November 2011 for porcupines at Site N.

Two porcupines were observed in close proximity to each other on July 29, 2011, though they did not visibly interact with the bone or dwell at the site for any length of time. During August, one porcupine interacted with numerous vertebrae, long bones, and the sacrum.

Photos from the researcher site visits demonstrate how heavily gnawed many elements of bone were **(Figures 4-6)**. Elements gnawed included the mandible, pelvis, vertebrae, and multiple long bone shafts.

Other Scavenger Activity

A coyote visited on four separate days in October 5, 6, 8, and 27, 2011. It did not visibly interact with any bone on screen, and it did not appear to spend much time at the site, though it is possible that activity occurred off screen.

Collected bones

Mandibular fragments and a femur were collected from Site N on October 17, 2011. At this point, the mandible was found 14 feet from the location of the original pig remains, and the femur was found 16 feet away.

Sequence of Bone Modification

On June 28, 2011, no evidence of porcupine scavenging was visible during the researcher site visit or on camera. Before the next site visit on August 7, 2011, a porcupine had visibly gnawed on bone on five different days. Using the video footage, affected remains appeared to include vertebrae, long bone shafts, and a pelvis. Most of this gnawing occurred within a 38-minute window on August 4th.

Photographic evidence from the researcher site visit on August 7th further demonstrated the damage done during the porcupine's visitations. Several long bones had been extensively gnawed, as had two pelvic elements. The mandible had also been extensively modified, though at this point it was not yet fragmented **(Figure 4)**.

Figure 4. Mandible at Site N on August 7, 2011 after extensive modification by porcupine, particularly on the ascending ramus. Damage to the anterior is likely attributable to canids.

After the researcher site visit on August 7, only one additional instance of porcupine gnawing was observed on camera the following day. However, the researcher site visit on August 19th established that there had been additional damage to multiple elements, particularly multiple long bones, a pelvic element, and the mandible. These events were not apparent on camera. By this point, cancellous bone was exposed through extensive chewing through the compact bone on multiple elements **(Figure 5)**. Additionally, the mandible was heavily fragmented and had reached the state it was in when collected in October 2011 **(Figure 6)**.

Figure 5. Pelvic bone at Site N on August 19, 2011. Porcupine gnawing exposed cancellous bone.

The last documented instance of porcupine gnawing occurred on August 10, 2011, yet extensive damage was observed at the following researcher site visit on August 19, 2011. A site visit on June 29, 2012 showed considerably more damage to multiple long bone fragments, beyond what the collected femur and the photographs from August 19th represented. Porcupines appeared to be the most likely culprit based on the extent of the damage and that the damage was very similar in appearance to that on the collected bone fragments. However, since no cameras captured any scavenging activity beyond November 2011, no conclusions can be easily drawn from further study of this site.

Figure 6. Fragmented mandible at Site N taken on August 19, 2011.

Behavioral Events

Porcupines at sites M and N visited between March 26, 2011 and November 19, 2011, with no visible activity occurring between November 19, 2011 and March 25, 2012 **(Figures 1, 3, and 7)**. Activity at Site M demonstrated the widest range of active dates **(Figure 1)** during which a porcupine visited the site. Since porcupine behavior was tracked over one winter season at Site N and two winter seasons at Site M, this strongly suggests a seasonal component to porcupine behavior and mobility consistent within the literature.

The only instances of direct contact with bone were concentrated in July and August of 2011 at both Sites M and N **(Figure 7)**. At Site M, one instance of gnawing occurred in July, and three occurred in August **(Figure 1)**. At Site N, two instances occurred in July and four occurred in August **(Figure 3)**. Most visits at both sites were fairly short, based on the time stamps on the camera footage. However, two visits, one at Site M on July 27th and one at Site N on August 4th, lasted longer than 15 minutes.

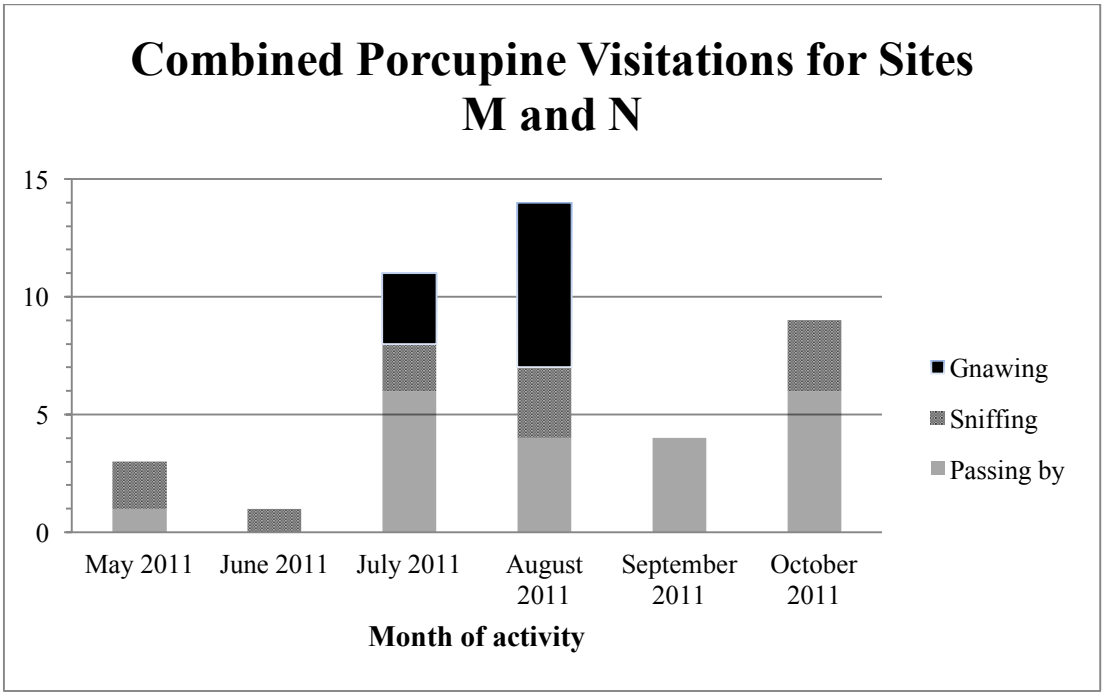

Figure 7. Number and type of behavioral events between May 2011 and October 2011 for porcupines at Sites M and N.

Summary of Variables

Seasonality and Salt Drive

Porcupine activity spanned the time from March to November, with a clear cessation from late fall to the beginning of spring. This is consistent with a winter

reduction in home range and mobility consistent within the literature. Roze's (2009) salt drive study suggested that porcupine gnawing, if driven by a need for salt, should begin in April and extend until October. Yet, the only observable instances of bone gnawing during my research occurred in July and August. This seems somewhat inconsistent with Roze's research. However, the delayed accessibility of dry bone at each site combined with apparent gaps in data, e.g., activity out of camera range, or not vigorous to trigger the camera, result in insufficient data to contradict Roze. Since the dates on which gnawing occurred fall within the range proposed by Roze, I believe that my observations may still align with Roze's data.

Winter Seasonality: Temperature and Snow Cover

As the literature suggested, freezing temperatures did not appear to be a primary indicator of porcupine activity. On eight days where temperatures fell below 32°F, a porcupine was observed passing by the site: November 2010, October 2011, March 2012 and April 2012. The lowest temperature during which a porcupine visited the site was 25°F, and a decrease in temperature over several days signaling winter may prompt porcupines to find dens, as Roze (2009) suggested.

A better indicator of winter porcupine activity may be snow cover. No winter activity occurred in the 2010-2011 season, but tracking Site M through the winter of 2011-2012 offered some insight into porcupine movement. The first snowfall occurred on October 29-30, and covered the ground with roughly two to three inches. The porcupine visited on October 30th and October 31st, briefly. The snow melted by November 4th. A porcupine next passed by the site on November 19th. Snow next

blanketed the ground on November 24th, and melted by the 29th. Snow again covered the ground on January 12, 2012 and lasted until March 20th, when it began to melt sufficiently that the pig's clothes were exposed. By the first porcupine visit of 2012 on March 26th, the snow had completely melted again. Snow again covered the ground by March 30th, which was the second porcupine visitation of the year, then melted entirely by April 8th, the day before the third porcupine visitation. Following this last snow melt, porcupines began intensively using the site, with nine visitations before May.

A porcupine only visited three times while snow was on the ground, and never when there were more than two to three inches, as was the case for most of January through March. Also, these visits occurred just after the first apparent snowfall and just before the last snowmelt. While this may simply correlate with other seasonal changes, it may also support the hypothesis that snow cover is an impediment to porcupine mobility and a primary factor in reducing winter home range.

Simultaneous Visitations by Multiple Animals

Only four porcupine visitations occurred in pairs. At Site N, the only dual-animal visitation occurred on July 29, 2011, when two porcupines passed through the site. However, at Site M on August 9, 2011, two porcupines spent at least six minutes at the site gnawing on bone. They remained in close proximity throughout the video footage, even gnawing on the mandible and possibly other elements together. Two porcupines passed through nine days later on August 18, 2011. Finally, a pair of porcupines was

observed sniffing around the site on April 19, 2012. Based on the size differential, this was likely a mother and her baby.

This solitary behavior is supported in the literature, which suggested that porcupines generally spend minimal time together under specific circumstances, so the proximity of the two porcupines observed together on August 9th is interesting. Roze (2009) observed multiple porcupines at the same salt lick on at least one occasion, but they were not in such close proximity to each other and maintained a healthy distance from each other. Because of their proximity, the two porcupines are likely either a mother and her baby or two males, at least one of which is subordinate. The two porcupines are unlikely to both be female outside of a mother-baby relationship, and August is too early for mating season to result in male-female pairs.

Avoidance of Predators

On multiple occasions, a porcupine visited the day after coyote or humans, supporting a limited avoidance of certain predators. At Site M, the first coyote visit occurred on August 23, 2011. The porcupine returned the next evening and stayed for several minutes. Another coyote visit occurred on October 22, with the porcupine returning on October 23, 2011 for several more minutes. At Site N, a coyote visit on October 8th preceded a visit by a porcupine only three hours later. Another visit by a coyote on October 27th was followed by a porcupine visit on October 29th.

At Site N, the first porcupine visit occurred on May 25, 2011, the day after I visited the site and replaced the standing orange flags with nails. A porcupine visited Site

N the day after another human site visit on August 19th. Also, after a researcher site visit on April 19th, a porcupine visited that evening.

In another instance on April 24, 2012, a porcupine and a coyote were observed in the same video footage. The porcupine, quills erect, quickly moved away from the site, while the coyote lingered for a moment in the next camera shot but was not caught on camera pursuing the porcupine. Following this encounter, the porcupine next returned on April 28th.

Porcupines did not linger long during any visitation immediately following a visit by a human or a coyote, with no visits lasting more than three minutes, though this was not atypical of the majority of porcupine visitations. At no other points did any porcupine demonstrate behavior as on April 24th when the visit coincided with that of a coyote, and the porcupine became alert and quickly moved away. The porcupine's highly developed sense of smell may simply allow it to interpret a lack of predators in the immediate vicinity, or it may simply lack an aversion to human and coyote scents. Alternatively, the scent of the coyotes and humans may have sufficiently deterred any scavenging. Since no fishers were present, I was not able to compare the response of the porcupine to the presence of fishers at either of these sites.

Other Variables: Precipitation and Time of Day

No porcupine visitations occurred during any precipitation. On all but two occasions (May 4, 2012 at 6:43PM and July 27, 2011 at 7:37PM), the porcupines visited at night, supporting their generally nocturnal behavior.

Bone Modification and Behavior

Porcupines at both sites interacted with ribs, long bone, vertebrae, pelvises, and mandibles. At no point did they appear to modify any smaller bones such as phalanges or carpals. They also did not appear to gnaw on the cranium. While the margins of the mandible, in particular, were affected, the shafts of the long bone were also targeted.

At Site N, despite the presence of two porcupines over a 30 minute period of time, damage to bone was relatively minimal during July and August 2011. Since the bone was heavily modified between November 2011 and June 2012, one possible explanation for this is that the bone was too fresh and the porcupines were less interested.

By contrast, one porcupine at Site M heavily damaged multiple bones in early August 2011. It chewed heavily along the margins of multiple long bones and completely fragmented the mandible.

The "buffet" behavior observed by Roze (2009, 70) seems to apply here. At the salt sticks, porcupines would sample multiple sticks within a block of time, without necessarily demonstrating a preference of focus. Similarly, the porcupine at Sites M and N do not seem to linger at one bone element for long before moving on to the next, then returning. Additionally, damage on each affected bone element may range from minimally marked to extensively fragmented **(Figures 2, 4-6)**.

Dentition

Incisor Measurements

My preliminary mid-crown width measurements of **(Table 1)** all spanned the range of Elbroch's data **(Table 2)**. However, as seen in **Figure 8,** the occlusal edge of the porcupine incisors can be highly irregular. To address this variation, I also measured each tooth just below the visible lip which divides the tip from the rest of the crown. On average, the difference between measurements for each incisor at the mid-crown location and the occlusal tip were 0.10 mm for the porcupine, 0.47 mm for the woodchuck, and 0.32 mm for the beaver. Variability between the mid-crown and occlusal tip measurements was consistently greater for lower incisors than upper incisors, though the range in variation was much narrower for the porcupine than for the other species.

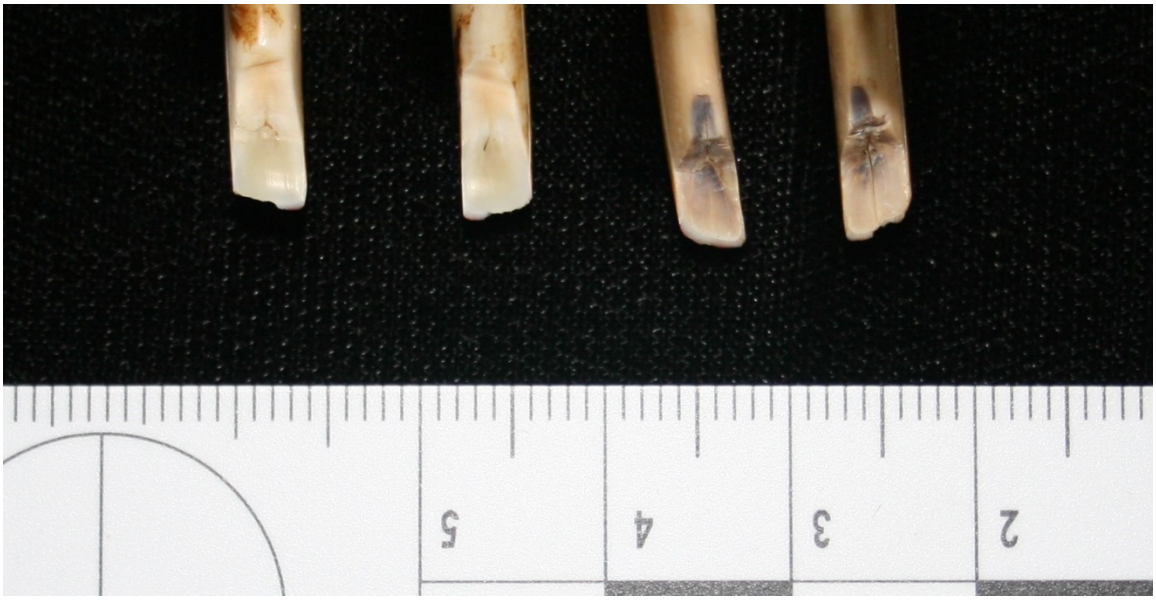

Figure 8. Lingual view of porcupine upper incisor from two specimens. Units are in centimeters.

Additionally, in one instance, the measurement at the tip of a porcupine's lower incisor (specimen 1) was greater than the mid-crown width, suggesting either a methodological flaw or a lack of consistency in incisor growth. Since I noticed this disparity while taking measurements, I re-measured the sample to rule out a methodological error, and the result did not change.

Table 1. Measurements of incisor widths from University of Maine Zooarchaeology Laboratory specimens. Parenthetical numbers adjacent to the species name identify individual animals.

Species (specimen)	Incisor location	Width mid-crown (mm)	Width at tip (mm)
North American porcupine (1)	lower	4.18	4.32
North American porcupine (1)	lower	4.23	4.20
North American porcupine (1)	upper	4.17	4.06
North American porcupine (1)	upper	4.15	3.95
North American porcupine (2)	lower	4.51	4.34
North American porcupine (2)	lower	4.59	4.47
North American porcupine (3)	upper	3.92	3.89
North American porcupine (3)	upper	4.00	3.77
North American porcupine (4)	lower	4.54	4.46
North American porcupine (5)	upper	4.14	4.14
North American porcupine (5)	upper	4.13	3.96
North American porcupine (5)	lower	4.09	3.86
Woodchuck/groundhog (1)	upper	3.85	3.35
Woodchuck/groundhog (1)	upper	3.92	3.32
Woodchuck/groundhog (1)	lower	3.62	3.25
Woodchuck/groundhog (1)	lower	3.54	3.13
American beaver (1)	upper	5.36	4.91
American beaver (1)	upper	4.98	4.49
American beaver (2)	lower	6.36	6.04
American beaver (3)	upper	7.66	7.22
American beaver (3)	upper	7.52	7.31
American beaver (3)	lower	7.38	7.24
American beaver (3)	lower	7.55	7.34

Table 2. Measurements of incisor widths for three species, compiled from Elbroch's (2006) data. All samples sizes are n=10.

Species	Incisor location	Average width (mm)	Minimum width (mm)	Maximum width (mm)
North American porcupine (female)	upper	4.32	3.81	4.89
North American porcupine (female)	lower	4.33	3.83	4.75
North American porcupine (male)	upper	4.23	3.63	4.72
North American porcupine (male)	lower	4.16	3.66	4.70
Woodchuck/groundhog (female)	upper	3.96	3.14	4.70
Woodchuck/groundhog (female)	lower	3.59	2.66	4.24
Woodchuck/groundhog (male)	upper	3.40	2.68	3.83
Woodchuck/groundhog (male)	lower	3.11	2.11	3.61
American beaver (female)	upper	6.61	4.95	7.71
American beaver (female)	lower	6.73	4.65	7.90
American beaver (male)	upper	6.71	4.89	7.98
American beaver (male)	lower	6.65	4.72	7.80

While the range of incisor widths among porcupines did slightly overlap with the range of woodchuck incisor widths, the greater variation among woodchucks in incisor crown widths at the occlusal tip may indicate an easier distinction between porcupine and woodchuck incisors than Elbroch's (2006) data would imply. However, one sample is insufficient to determine whether this pattern is consistent across all woodchucks, and Elbroch does not discuss varying degrees of wear on rodent incisors. Additionally, one anomalous beaver incisor is only 0.02mm greater than the largest porcupine incisor, and the beaver's greater range of incisor widths may also result in some confusion among smaller beaver incisors and larger porcupine incisors.

In summation, these data, in conjunction with photographs of porcupine incisors **(Figure 8)**, strongly suggest that uneven wear patterns in incisors pose substantial challenges to the possibility of identifying particular species based on measurements of gnaw marks, since the width of gnaw marks would most closely resemble the tips of the incisors, and variations in incisor wear may result in additional overlap in incisor widths across species.

Measurements of gnaw marks on collected bone

I took measurements of gnaw marks on three mandibular fragments and the femur. Careful examination resulted in some grooves that were wider and more clearly defined than others. On the mandibular fragment, shown in the lower right corner of **Figure 9**, the clearest measurement resulted in an estimated width of 4.87mm. On the left mandibular fragment with teeth, depicted on the middle right of **Figure 9**, a groove on the interior margin resulted in an estimated width of 3.49 mm. The right mandible had several deep grooves on the ascending ramus, in the notch just beyond the final molars. Three measurements in three different grooves in this region resulted in measurements of 3.43mm, 4.33mm, and 4.40mm. Five measurements from grooves on the femur **(Figure 10)** ranged from 3.84mm to 4.32mm.

Figure 9. Mandibular bone fragments of scavenged domesticated pig (*Sus scrofa*) from Site N, heavily gnawed by porcupine.

Figure 10. Posterior view of collected right femur of scavenged domesticated pig (*Sus scrofa*) from Site N, heavily gnawed by porcupine.

Although these measurements ranged from 3.43mm to 4.87mm, only two mandibular measurements fell below the range expected based on known incisor widths.

However, multiple smaller measurements were taken at the site, including one of 1.45mm and 2.32mm on the femur. Large patches of surface were too smooth to determine where one groove began and ended and significant overlap in tooth marks exacerbated the challenge of this task. Additionally, variations in the occlusal surface of the porcupine's tooth likely contributed to the obfuscation of clear grooves, and may have created 'faux' edges. The most well-defined mark was likely on the anterior aspect of the femur, where one mark appeared to be the final in a series of gnaw marks, based on its clearly defined ridges, resulting in the widest measurement on that bone element (4.32mm).

While the overall pattern of gnaw marks obviously resembled that of other rodents, only the relative width of the marks indicate a larger rodent is responsible. The overlapping markings and ambiguity in ridge definition result in measurements too inconsistent to definitively conclude that a porcupine created those gnaw marks. Without the photographic evidence, the clearest measurements of the incisor damage can, at best, lead to a strong inference that a large rodent was responsible, most likely a porcupine or a woodchuck given the overlapping incisor widths among their populations.

DISCUSSION

Variables Impacting Porcupine Seasonality

Over the course of my study, seasonality had the greatest impact on porcupine activity, essentially precluding all winter activity. While temperature cannot be ruled out as a factor, snow cover may limit mobility the most and be the best way of predicting when porcupines may emerge from their dens. In determining activity outside of winter in forensic contexts, based on the literature, I would suggest that salt drive may provide the best explanation.

Despite Roze's (2009) research on salt drive, I only observed direct contact with bone during July and August. One likely explanation is that the porcupine demonstrates a strong preference for dry bone, as indicated by the literature and supported by the greater bone modification at Site N compared to Site M. This would have prevented the porcupine from gnawing on bone in April and May, when Roze observed the greatest surge in sodium-driven gnawing, since the remains were still being defleshed during that time. The porcupines may have then waited until the bones dried out sufficiently. This seems likely based on the minimal mandibular modification at Site M, which occurred in conjunction with a peeling pattern unseen in any other context during this study **(Figure 1, on the mandibular body inferior to the molars).** While it is unclear whether or not this damage was caused by the porcupine, the presence of this thin layer of periosteum likely indicates that the bone is still fresh.

This distinction appears to be significant to the porcupine, since these bones are barely modified compared to the extensive damage on the bones at Site N around the

same time. Possibly, fresher bone is more challenging to gnaw for the porcupine, or otherwise deters gnawing. Additionally, in lieu of photograph evidence during this period, I speculate the heavy gnawing damage that was observed at Site M between November 2011 and June 2012 most likely occurred between late March and early June, during the prime months for a porcupine's salt drive because the bone had sufficiently dried at that point.

Alternatively, seasonal salt drive may vary between porcupines in the Catskills, where Roze researched, and the western Maine woods. Dietary differences in sodium and potassium intake and varying access to natural sodium sources may result in unique regional fluctuations in salt drive. However, it does seem probable that female porcupines require increased amounts of sodium while gestating and weaning, particularly between May and April, since newborn porcupines gain weight quickly and place additional nutritional pressure on porcupine mothers.

Bone Modification and Behavior

The porcupine displayed fairly distinctive patterns of bone modification. They did not visibly scatter bone, though they did pick up bone elements to gnaw on them. Porcupines were observed gnawing extensively only on dry bone, with a focus on long bones, the pelvis, and the mandible, with an occasional rib and vertebrae. They often switched between elements. Modification ranged from minimal markings to extreme fragmentation, which could happen within a short window of time, as seen at Site N

when the mandible fragmented between August 7th and August 19th, despite only one event of porcupine gnawing during that time.

Porcupine behavior falls neatly within the broad context of rodent literature, which describes a variety of possible behaviors across species **(Table 3)**. Based on porcupine literature and my own observations during this study, porcupines do not appear to cache or collect bone elements, like packrats or Old World porcupines, though more research must be done to effectively eliminate this possibility. Porcupines do not appear interested in gnawing on soft tissue, unlike many smaller rodents.

Porcupine markings on bone are consistent with those of other rodents, though they may cause more extensive damage than many smaller rodents. Also, I did not observe any "fan-shaped gnawing" patterns as Nawrocki (2009) observed with smaller rodents, only roughly parallel gouges, which seems consistent with patterns of larger rodents. Gnaw marks were extensive enough and smooth enough to obscure the margins of bone elements and interfere with their identification. Additionally, porcupines at Sites M and N were uninterested in the epiphyses of any long bone, and intense porcupine gnawing cut through bone mid-shaft down to the cancellous bone, unlike many smaller rodents who focus on gnawing through metaphyses to access cancellous bone.

Table 3. Porcupine and rodent literature compared to observed porcupine behavior in this study.

Variable	Observed porcupine behavior in this study	Porcupine literature (Roze 2009)	Rodent literature (Haglund 1992; Nawrocki 2009; Pokines 2014)
Seasonality of bone gnawing	Gnawing occurred in July and August.	Based on salt drive research, expected heavily in April and May, tapering off through October.	Heavily dependent on type of rodent and context of remains.
Type of bone affected	Definite focus on dry bone.	Roze observed a porcupine gnawing on the bones of a freshly dead deer (2009).	Larger rodents more likely to gnaw on dry bone.
Elements affected	Mostly long bone and mandible, no smaller elements or skull; Sampling of various bone elements observed.	N/A. However, they will rotate between multiple sources of sodium at site like a "buffet" (Roze 2009, 70).	For larger rodents, most likely exposed margins of dense bone. For smaller rodents, margins with and epiphyses, with emphasis on access to cancellous bone.
Morphology of gnaw marks	Generally in parallel striations along margins. Channels are wide and smooth and not easily discernable.	N/A.	Often parallel striations. Larger rodents create smoother and more irregular surfaces; smaller rodents create narrower channels and may exhibit fan-shaped patterns.
Displacement of bone	Localized gnawing only, no bone movement.	Local gnawing, minimal bone displacement. Some speculation that bone may be brought back to dens for young pups, but no substantiation.	Some species may carry bone back to their dens. Many others will displace bone by burrowing near remains.

Identifying Porcupine Activity at Forensic Sites

Much of the literature on rodent activity suggests that their behavior is too variable to form anything but generalizations unless speciation is done. Porcupines are unique in part because they fall among the few larger species of rodents, so distinguishing them from their compatriots should be simpler than distinguishing among smaller rodent species. Although a definitive identification of porcupine activity at a forensic site is unlikely, there are multiple diagnostic characteristics than can support inferences of porcupine activity in forensic contexts.

Estimations of incisor width based on direct measurements of gnaw marks may lack consistency and overlap with other species, such as the woodchuck and the beaver. Conveniently, there have been no observations of the American beaver gnawing on bone, and a recent study suggested the American beaver does not have a salt drive (Strules 2012), further reducing the likelihood of beaver involvement. Woodchucks, however, do have a seasonal salt drive (Weeks and Kirkpatrick1978), and cannot be eliminated as a potential cause of scavenging. Studies of woodchuck activity may reveal seasonal differences in behavior or salt drive that can reduce the possibility of woodchuck at a forensic site. Additionally, comparative studies of woodchuck modifications on bone or other surfaces may demonstrate variations that would improve diagnostics. However, because woodchucks do have smaller incisors on average and they have not been observed gnawing on bone, finding relatively wider gnaw marks and greater damage are likely sufficient to infer porcupine modification. Careful measurements of striation widths may indicate porcupine activity when they exceed approximately 3.5mm.

Additionally, at Site N, several porcupine quills were collected from the site. In lieu of other evidence, quills provide evidence of the animal's presence at the site, though not evidence of gnawing itself. Insight into when the remains were placed may determine whether a porcupine had the opportunity to gnaw on bone, and fresher bone may preclude the likelihood of extensive porcupine gnawing. Also, porcupines appear likely to sample and modify a variety of larger bones at a site, without impacting the skull or any smaller bone fragments.

Although a definitive determination of porcupine activity at a forensic site is unlikely, there are multiple indicators and diagnostic characteristics than can support inferences of porcupine activity in forensic contexts (**Table 4**). Such characteristics include gnawing patterns which emphasize flat bones and mid-shafts and demonstrate extensive, wide parallel striations which obscure bone margins and sometimes fragment bone. Additionally, the presence of porcupine quills, porcupine gnawing on nearby trees, and any porcupine track marks may indicate a porcupine's presence in the area, increasing the possibility that gnaw marks are attributable to porcupine.

Table 4. Possible indicators and diagnostic characteristics of porcupine activity in forensic contexts based on my review of the literature and observation during my study.

Possible indicators of porcupine activity
Porcupines are unlikely to be active in winter, especially while snow is on the ground.
Temperature does not appear to restrict porcupine activity.
Precipitation may preclude porcupine activity.
Most, though not all, porcupine activity will occur at night.
Porcupines are usually solitary, but may spend time in pairs.
Porcupines will not avoid areas where humans or coyotes have been.
Likely diagnostic characteristics at forensic sites
Porcupines will primarily modify bone once it is dry.
Porcupines will sample multiple bones at a forensic site, generally long bones and flat bones.
Porcupine damage may vary from minimal to extensive in fairly short amounts of time.
Porcupine modifications may obscure margins and even fragment bone.
Porcupine gnawing creates smooth surfaces with poorly defined ridges that do not easily indicate width. However, channel widths over 3.5 mm may be reflective of porcupine incisors.
Porcupines do not focus on accessing cancellous bone, although exposure of cancellous bone may occur after extensive gnawing.
Porcupine gnaw marks will most likely appear as parallel striations, not as fan-shaped patterns.
Porcupine will not scatter bones, though they will slightly dislodge them.

Limitations of Methodology and Further Areas of Study

While the data from this study highlights an area of research that has been underdeveloped, it is far from a comprehensive overview of porcupine scavenging behavior. Variations in animal behavior and environment may limit the applicability of many taphonomic studies to other regions. Since my taphonomic data was collected from western Maine, my results may only be applicable locally, or with caution across regions.

As previously discussed, I only observed bone gnawing during two months of the year, which probably does not reflect the full range of dates during which bone gnawing may occur, especially in areas, or during winters, with less snow, nor does it reflect the relative intensity of bone gnawing across the year. However, the complete lack of

activity in winter months is likely reflective of a seasonal pattern, and observed behavioral patterns are reflective of those in literature. Since scatter was prevalent prior to any porcupine involvement, and a coyote at Site M continued to scatter the remains throughout the period of the study, the cameras likely did not capture all scavenging activity at each site. Also, since the camera at Site N began capturing hourly photographs in November 2011 rather than capturing motion, the data set ends earlier than at Site M.

Although I used sniffing behavior as a loose indicator of porcupine interest in the pig remains, porcupines also rely heavily on their sense of smell to navigate their environment, so sniffing behavior may not accurately reflect an interest in the remains. While photographic evidence throughout 2011 is sufficient in some cases to determine if porcupines' attention is on the remains, Site M is overrun by foliage in 2012, obfuscating visibility of any remaining bone elements and making it impossible to determine if the animal is interested in them or in other aspects of the environment.

While I did not observe any obvious indicators that the porcupines avoided coyote or human scents, I also did not observe any fishers at either site. Since Osburn and Cramer (2013) suggested that porcupines most strongly avoid fisher, studying visitation patterns in conjunction with fishers at a site would provide a valuable comparison for porcupine behavior in proximity with coyotes and humans. There is also no way to determine how effective the clothes were in infusing the remains with human scent. If the scent faded by the first porcupine encounter, then this study may not represent how a porcupine might interact with human remains. However, the propensity of porcupines to approach man-made sources of sodium (Roze 2009) suggests that porcupines may not avoid other sources of human scent.

Overall, this set of data was insufficient to describe seasonal porcupine behavior at forensic sites. The small sample size necessitated a descriptive analysis, but additional quantifiable research could allow for statistical analyses which would improve descriptions of porcupine behavior. I recommend further research approaching porcupine scavenging in a similar fashion, with at least two motion sensitive cameras to specifically identify porcupine visitation patterns. Such research should ideally span multiple years to account for annual variabilities and should consider regional variations in dietary requirements. Future studies should address the seasonality of the porcupine's salt drive in more depth, possibly by staggering the placement of bone elements (or other salt sources) throughout the year. Furthermore, research should expand on my observations of bone modification patterns to better define diagnostic features of porcupine scavenging.

More research is also necessary to determine whether snow cover is predictive of porcupine mobility and how the presence of predators might influence porcupine behavior. Yet, capturing direct evidence of bone gnawing by a North American porcupine is a significant triumph considering the dearth of evidence in literature, and the data offered valuable insights into the impact porcupines may have in forensic contexts. Further research should certainly expand on seasonality and patterns of bone modification and address specific behavioral patterns.

CONCLUSIONS

This study involved a close examination of porcupine behavior at two sites of pig cadavers in western Maine forests. Variables studied included the number of animals, the bone elements affected, and the behavioral event, which I connected to factors such as snow cover, temperature, the condition of the remains, and seasonality. Following this, I examined a mandible and a femur that were directly gnawed on by porcupines at one of these sites and connected measurements of these gnaw marks to widths of incisors in literature and from the University of Maine Faunal Lab to assess the possibility of identifying porcupine-modified remains from the gnaw marks alone. These data provided valuable insight on bone modification by the North American porcupine, which has rarely been studied. However, significantly more research must be done to draw conclusions regarding porcupine behavior at forensic sites.

The literature suggests that the porcupine is most likely to be active from the early spring to late fall, when no snow is present on the ground, which the photographic evidence in this study supported. However, a porcupine's salt drive appears to be a critical component when addressing the seasonality of a porcupine's bone modification, since it prompts the animal to gnaw on bone. More research must occur to connect their seasonality with their salt drive within local ecologies because of regional variations in diet. However, my research demonstrates that Maine porcupines do gnaw on bone during July and August, which could be directly connected to their salt drive.

This research confirmed that bone modification by the North American porcupine is consistent with overall rodent patterns, as evidenced by the gnawing patterns found at both research sites. As demonstrated in the literature, markers of bone modification by the North American porcupine include closely striated patterns reflective of their dental morphology, similar to modifications by other rodents. However, the porcupine also diverges from other rodents in several ways. It prefers bone without soft tissue attached and can cause heavier damage more rapidly, sometimes resulting in significant fragmentation to bone elements, as demonstrated at Site N. There appears to be no direct evidence that the North American porcupine collects bone in literature, and I could find no evidence of this in my observations. The porcupine is distinct from smaller rodent species since it does not nest within the remains, as some smaller species do, nor does it create fan-shaped striations. Based on the differential patterns at Sites M and N, porcupines appear to prefer drier bone over fresh bone, as suggested by the literature.

Although porcupine incisors are significantly wider than most rodents, I do not believe that gnawing damage will not allow conclusive proof of porcupine activity. Since the only rodent with wider incisors (the American beaver) does not modify bone, porcupine activity could be inferred from the extent of the damage and the width of striations on the bone. However, direct measurements of these gnaw marks are not consistent enough to conclusively determine if a porcupine was their origin, particularly since their incisors are so similar in width to those of woodchuck. Patterns of bone gnawing, including modifications primarily of long bone shafts and parallel rather than fan-shaped striations, may offer additional support for porcupine activity. Quills found at

the site and other animal markings may also confirm the presence of a porcupine, though this may only be used to support other markers of porcupine activity.

Distinguishing porcupine modification from that of other rodents or scavengers at forensic sites can be taphonomically valuable. The seasonality of porcupine activity and its localized activity may allow for inferences regarding the scatter of remains and estimations of time since death. For example, since porcupines appear to modify bone only after it has dried, evidence of porcupine gnawing could provide insight into the length of time the remains were exposed, and knowledge of porcupine activity in conjunction with heavily scattered remains would indicate that other scavengers were present at the site. Also, correct identification of porcupine damage is essential when attempting to determine cause of death, so gathering observations of porcupine bone modification can allow for better comparisons with other forms of damage. While more research must be done to accurately match porcupine activity with seasonality and rule out certain behavioral patterns, this research may provide significant insight into forensic sites where porcupine activity is discernable.

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